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RESEARCH PAPER

Soil seed bank assembly following secondary succession on abandoned agricultural fields in Nicaragua

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Abstract: The composition and density of seeds in soils of secondary forests derived on abandoned fields after 4, 9 and 14 years of abandonment were quantified to examine whether the soil seed bank assembles during secondary succession as the plant communities assemble. A total of 18, 37 and 48 soil samples from 4-, 9- and 14-year old sites, respectively were collected in 15 cm × 15 cm plots up to 9 cm depth. A total of 3, 5 and 9 species were found on sites abandoned 4, 9 and 14 years ago, respectively. Among different life forms, trees were highly represented in the soil seed bank of 9-year (60%) and 14-year (33%) old sites compared to 4-year old site entirely dominated by non-woody flora. The total number of seeds ranged from 327 in the 4-year old site to 146 in the 14-year old site, and the corresponding density of viable seeds ranged from 141 seeds $\cdot m^{-2}$ in the 4- year old site to 26 seeds m^{-2} in the 14-year old site with a consistent decreasing pattern in the chronosequence. The similarity between the soil seed flora and the standing woody vegetation was low for both 9- and 14-year old sites while complete dissimilarity was found for 4-year old site. We concluded that the species composition of soil seed banks assemble gradually during secondary succession, but the overall seed density is still low for natural regeneration of trees to rely on. To expedite the recovery of secondary forests on such abandoned fields, the seed bank needs to be supplemented by direct seeding, enrichment planting of desired species and installing artificial perches for facilitating seed dispersal.

Keywords: seed dispersal; dry forest; seed bank; secondary succession; restoration; Nicaragua

Introduction

Large tracts of crop and pasture fields have been abandoned in many parts of Central and Latin America due to a shift in the economic interest (Thomlinson et al. 1996; Jansen 2002). In the past, such abandoned fields have largely been neglected. However, tropical secondary forests derived from abandoned fields have gained much attention owing to their socio-economic (Chazdon and Coe 1999; Chokkalingam et al. 2001) and ecological importance (Lamb et al. 1997; Silver et al. 2000) as well as their fast-growing ability and the current pressure on remaining old-growth forests (Finegan 1996; Sips and Linden 1998; Guariguata and Ostertag 2001). Thus, an understanding of barriers for secondary succession on such lands is important for expediting the recovery process.

Initially, the recovery of secondary forests on abandoned fields is dependent on the availability of seeds (Zimmerman et al. 2000; Wijdeven and Kuzee 2000; Holl et al. 2000). Seed availability can be characterized by the presence, gain, and loss of viable seeds. The presence is confined to the viable seed bank, which may be altered by the duration, frequency and intensity of disturbance (Teketay 1997; Tekle and Bekele 2000; Luzuriaga et al. 2005; Lemenih and Teketay 2006). The gain refers to recent seed dispersal (seed rain) into the site, which may be affected by the availability of propagule donors (Teketay and Granström 1995; Teketay 1997). Loss of viable seeds may be caused by factors such as germination; unfavorable environmental conditions resulting in decay and senescence of seeds, as well as predation and pathogen infection (Dalling et al. 1997; Teketay and Granström 1997; Hau 1997; Wijdeven and Kuzee 2000; Murray and Garcia 2002).

Soil seed bank can serve as "succession primer" for secondary regrowth on abandoned or degraded sites, depending on the frequency and severity of previous disturbance. The soil seed bank refers to all viable seeds and fruits present on or in the soil and associated litter/humus. Soil seed banks can be either transient,

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with seeds that germinate within a year of initial dispersal, or persistent, with seeds that remain in the soil for more than a year (Simpson et al. 1989). They exhibit spatial and temporal variations, reflecting their initial dispersal onto the soil and subsequent movement (Simpson et al. 1989). The pool of long-lived seeds in the soil accumulates over many decades and forms a source of propagules that ensures continual occupation of a site after disturbances, while serving as a gene pool by buffering genetic changes in the population. During secondary succession, the soil seed bank assembles as result of the balance between seed input and seed output at the same time as the plant community assembles (Fenner 1985; Mengistu et al. 2005). Thus, information about soil seed bank dynamics of secondary forests in a chronosequence is of paramount importance to decide whether active or passive restoration approaches should be employed to foster the recovery of secondary forests on abandoned fields. While passive restoration is largely dependent on natural regeneration processes with minimal or no intervention, active restoration entails all sorts of facilitation to assist the natural processes; such as direct seeding, enrichment planting, artificial seed dispersal facilities, site manipulations etc (Holl et al. 2000).

As in many Central American countries, most forest lands in Nicaragua were clear cut and put into production of agricultural crops (beans, maize, and rice) and pasture in the 1960s (Per. comm. with key informants). In recent years, agricultural and grazing activities were abandoned, and there is a general consensus among land owners to let the abandoned sites recover and be transformed into secondary forests in order to meet their demands for fuel wood and construction poles (Anonymous 1994). Since studies on secondary forest succession on abandoned sites are not available in Nicaragua, it may not be possible to predict whether abandonment of agriculture after different years and intensities of cultivation could potentially result in the development of secondary forests from the soil seed bank. Thus, this study was initiated to examine whether the soil seed bank assembles during secondary succession; thereby contribute to the recovery of woody vegetation on abandoned sites. The specific objectives were to; (1) describe species composition and density of the soil seed flora in a chronosequence of 4, 9, and 14 years after abandonment and (2) compare species similarity between the soil seed flora and the standing woody vegetation. We hypothesized that species composition of the soli seed bank increases with increasing age of abandonment of cultivated fields due to improved seed rain from pioneer species colonized the site and better conditions for seed dispersing agents, whereas viable seed density declines due to seed loss by predation, decay and senescence as well as germination.

Materials and methods

The study site

The study was conducted in the village of La Chipopa (11°42’30’ N and 86°05’30’ W), located at 7 km south of the city of Nandaime in Granada Province along the Pacific region of Nicaragua (Fig. 1). The study site was initially owned by a sugar cane factory, called Amalia, and the forest was exploited for firewood production to heat the boilers of the sugar cane factory. Later on, the owner rented out the land to farmers for producing agricultural crops. During the Sandinista agrarian reform, the land was allocated to a group of farmers who constituted the Martin Cortez cooperative. The farmers abandoned farming and pasture development in the 1990s and let the fields to rest. The site receives a mean annual precipitation of 800−1 200 mm, with a mean annual temperature ranging between 27°C and 29°C. The dry season spans over six months from November to May. The soils of the area are loamy or loamy franc on the surface and loamy in the sub-surface with a pH of 7 (Anonymous 1994). For the present study, three crop fields, which have been under cultivation since 1965 and abandoned 4, 9 and 14 years ago, were selected with the assistance of key informants (Mario Soza and Carlos Soza). Currently, the abandoned sites support young secondary forests. The species composition, structure and diversity of these young secondary forests are reported elsewhere (Castro-Marin et al. 2009). The size of the study sites was 1, 3.7 and 4 ha for 4-, 9- and 14-year old patches, respectively (hereafter referred to as site-4, site-9 and site-14).

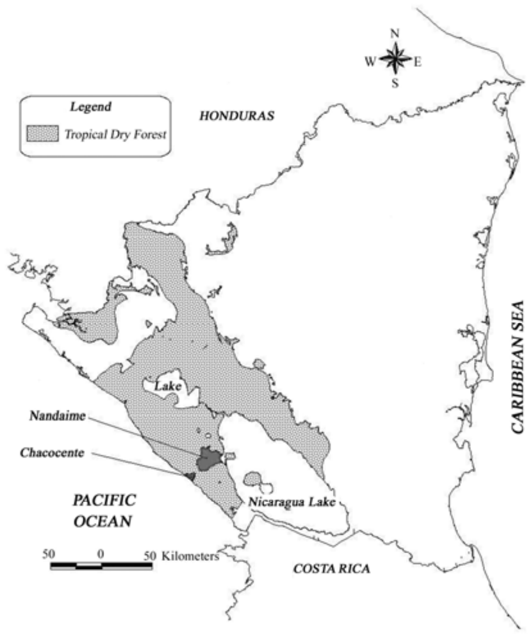

Fig. 1 Location of the study area in the vicinity of Nandaime. Close to the study site is the well-known Chacocente Wildlife reserve.

Soil seed bank sampling

In early June 2004, 18, 37 and 48 soil samples from site-4, site-9 and site-14, respectively were collected in 15 cm × 15 cm plots. The number of soil samples taken from each site was different mainly due to variation in size of each site and the intent to obtain representative samples. The distance between any two consecutive plots was 40 m. In each plot, four separate soil layers were removed using a sharp knife and a spoon and put into cloth bags. These layers included litter layer and three successively

deeper mineral soil layers at a depth of 3 cm. Soil samples were sieved using a mesh size of 0.5 mm, and seeds recovered from all sample plots were identified to species level and according to life forms with the help of a botanist and an agronomist at the National Agrarian University in Managua, Nicaragua, and nomenclature follows Salas (1993).

To determine the viability of recovered seeds, a germination test was carried out on Jacobsen's apparatus at 20ºC ± 2ºC with an illumination of ca. 20 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fluorescent lamp F 40 W / 33 RS cool white light) for six weeks at the Seed laboratory in Umeå, Sweden. The number of germinants was counted every two days when the radicle reached 2 mm and had a normal appearance. After the germination test was terminated, seeds remaining ungerminated were further assessed for their viability by cutting test. Seeds were considered viable if their content was white and firm while seeds covered with fungi, collapsed when pinched, and having grey, yellow, or brownish contents were considered as dead (Teketay and Granström 1995; Baskin and Baskin 1998).

Vegetation sampling

Parallel with the seed bank sampling, an inventory of the standing vegetation was carried out using nested design. On each site, 10 m × 10 m plots were laid out to record individuals with diameter at breast height (DBH) ≥10 cm. Plots of 5 m × 5 m were used for recording individuals above 1.5 m height and below 10 cm DBH, and plots of 2 m × 2 m were used for recording individuals from 30 cm to 150 cm height.

Data analysis

The species found in the soil samples were classified according to their life form as trees, shrubs, liana, herbs and grasses. The species composition, number of seeds and density of viable seeds in the soil were determined for each abandoned site. The number of viable seeds was determined by combining the germination and cutting tests. The density of viable seeds was then computed as the number viable seeds divided by area sampled and standardized per unit area. As the number of seeds recovered per plot at each depth was few, seeds from all plots and depths were pooled by species, and Chi-square analysis was performed to determine whether the observed seed density and species composition vary with age of abandonment. Similarity in the soil seed flora among sites, as well as with the standing woody vegetation and isolated remnant trees for each site was compared using Jaccard's similarity coefficient (Krebs 1998).

Results

Species composition and seed density in the soil

A total of 14 species, distributed among 10 families, were recovered from the soil samples, representing trees, shrubs, herbs, grasses and lianas (Table 1). Poaceae made up the dominant family with four species, followed by Rubiaceae with two species. Composition of seed bank species varied significantly among abandoned sites in a chronosequence ($\chi^2(0.05, 2) = 22.455$; $p < 0.001$). The youngest site had few seed bank species while the oldest stand had several species (Table 1). The seed bank of site-4 was dominated by a single grass species; *Bouteloua alamosana* Vasey while a tree species, *Guazuma ulmifolia* Lam., dominated the soil seed bank of site-9 (Table 2). The seed bank of site-14 was represented by many species with few seeds and only *Hybanthus attenuatus* (Humb. & Bonpl. ex Roem. & Schult.) Schulze-Menz had a relatively higher seed density (Table 2).

Table 1. List of seed bank species together with number of seeds recovered from soil samples of three secondary forests developed after 4, 9 and 14 years of abandonment of agriculture and their viability.

Seed bank species	Family	Site (age)	Total no. seeds	Viability (%)
Bouteloua alamosana (g)	Poaceae	4	47	91
Cynodon dactylon (g)	Poaceae	4	105	2
Hybanthus attenuatus (h)	Violaceae	4	175	7
Mocuna priarens (l)	Fabaceae	9	10	100
Hybanthus attenuatus (h)	Violaceae	9	83	2
Guazuma ulmifolia (t)	Sterculiaceae	9	35	83
Karwinskia calderonii (t)	Rhamnaceae	9	22	100
Genipa Americana (t)	Rubiaceae	9	6	17
Sorghum halepense (g)	Poaceae	14	27	22
Lantana camara (s)	Verbenaceae	14	6	17
Stemmadenia obovata (t)	Apocynaceae	14	18	6
Casearia corymbosa (t)	Flacourtiaceae	14	4	25
Chomelia speciosa (t)	Rubiaceae	14	44	7
Bouteloua alamosana (g)	Poaceae	14	7	29
Mocuna priarens (l)	Fabaceae	14	6	67
Cenchrus echinatus (g)	Poaceae	14	16	25
Sida sp.(h)	Malvaceae	14	18	11

(g):grass; (h) : herb; (l):liana; (s): shrub; (t):tree

Table 2. Species with seed density ≥ 10 seeds/m2 in the soil samples collected from three secondary forests developed on sites abandoned 4, 9 and 14 years ago in Nicaragua.

Abandoned sites	Species	Life form	Seed density
Site-4	*Hybanthus attenuatus*	herb	30
	Bouteloua alamosana	grass	106
Site-9	*Mocuna priarens*	liana	12
	Bouteloua alamosana	grass	23
	Karwinska calderonii	tree	26
	Guazuma ulmifolia	tree	35
Site-14	*Hybanthus attenuatus*	herb	11

The total number of seeds recovered from the soil samples and the corresponding density of viable seed significantly varied among abandoned sites in the chronosequence ($\chi^2(0.05, 2) =$

24.733, $p < 0.001$ for seed number; and $\chi^2(0.05, 2) = 439.841$, $p < 0.001$ for seed density). The total number of seeds was 327, 156 and 146 for site-4, site-9 and site-14, respectively (Fig. 2A). The corresponding density of viable seed decreased from 141 seeds m^{-2} in site-4 to 76 seeds m^{-2} in site-9 and 26 seeds m^{-2} in site-14 (Fig. 2B). For most of the species, the viability of seeds recovered from the soil samples was low.

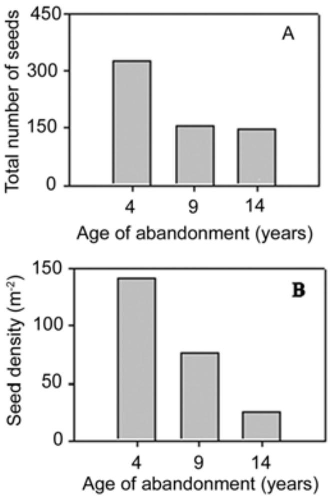

Fig. 2 Total number of seeds (A) and density of viable seeds (B) in soil samples collected from three secondary forests developed on sites abandoned 4, 9 and 14 years ago in Nicaragua.

Similarity in species composition

The similarity in soil seed flora was relatively higher between site-4 and site-9 than between site-9 and site-14, and between site-4 and site-14 (Table 3). When the species composition of the soil seed bank was compared with the standing woody vegetation, the coefficient of similarity was low for both site-9 and site-14; whereas no similarity in species composition was found for site-4 (Table 4). The soil seed flora and the isolated remnant trees also exhibited low similarity in both site-9 and site-14, and complete dissimilarity in the site-4 (Table 4). *G. ulmifolia* was the only woody species that was common to both the soil seed bank and remnant trees in site-9. In site-14, *Chomelia speciosa* Jacq. was represented in the soil seed bank as well as in the population of remnant trees.

Discussion

The species composition of soil seed banks markedly differed in a chronosequence. The total number of species recovered from soil samples increased with increasing age of abandonment. Grasses and herbs were more abundant in site-4 while trees were dominant in the soil seed banks of site-9 and site-14. Generally, two possible pathways can be distinguished for a seed bank assembly process during succession: (1) the seed bank is mainly composed of early successional species that accumulate many persistent seeds in the soil even after the species disappear in the vegetation and (2) the seed bank composition varies as the standing vegetation changes. In the second case, although early successional species disappear from the seed bank as they disappear from the standing vegetation, the seed bank gradually assembles as a result of seed rain from species appearing later during succession and/or from isolated remnant trees and recent seed dispersal from the nearby vegetation (Beatrijs and Martin 2004). It is evident from the present study that the number of species, especially the woody flora, in the soil seed bank increased as succession advanced (Table 1). Most likely, the assembly of the soil seed bank observed in the present study followed the second pathway. First, the isolated remnant trees present on site-9 and site-14, and individuals that could reach reproductive maturity might contribute to the build-up of the seed bank through seed rain (Guevara et al. 1986; Holl 1999; Wijdeven and Kuzee 2000). Second, both remnant trees and individuals reached reproductive maturity possibly attract seed disperser (mainly birds and bats); thereby facilitating recent seed dispersal to the site (Wunderle 1997; Guevara et al. 2004). Several studies have shown that zoochorous dispersal agents do not readily cross or enter open sites due to lack of food resources, perching sites, and visibility to predators (Aide and Cavelier 1994; Nepstad et al. 1996; Wunderle 1997; Guariguata and Ostertag 2001).

Table 3. Comparison of similarity in soil seed flora among three secondary forests developed on sites abandoned 4, 9 and 14 years ago at each site using Jaccard's similarity coefficient (Sj %)

Abandoned sites	common species	S_j
14 years vs. 9 years	1	8
14 years vs. 4 years	1	9
9 years vs. 4 years	1	14

Table 4. Comparison of similarity in soil seed flora between soil seed flora and standing woody vegetation and isolated remnant trees at each site using Jaccard's similarity coefficient (Sj %)

	Standing woody vegetation			Isolated remnant trees		
Seed bank	4	9	14	4	9	14
4	0.0			0.0		
9		6.6			10	
14			7.0			14

Unlike species composition of the seed bank, seed density decreased with increasing age of abandonment (Fig. 1). The density of buried seeds is a result of the balance between seed input (local seed production and seed dispersal) and seed output, i.e. seed germination, decay and predation (Fenner 1985). The large quantity of seeds recovered from soil samples collected on site-4 could be related to large quantity of local seed production by herbs and grasses (Table 2). However, as secondary succession advances, herbs and grasses are replaced by pioneer, light-demanding species (Finegan 1996) and hence the seed input started to decline. For example, the seed density of *H. attentuatus* declined from 30 seeds m^{-2} on site-4 to 11 seeds m^{-2} on site-14. Seed predation is another important determinant of seed bank size (Uasuf et al. 2009). Several studies have shown that predation rates are higher in forest than in open grasslands (Aide and

Cavelier 1994; Kollmann and Pirl 1995; Hau 1997), but others still found the opposite trend (Nepstad et al. 1996) or detected no major differences (Holl and Lulow 1997), most likely related with the type of seed predators – rodents are major seed predators in the forest while insects in the open site. The soil seed bank could also be depleted by germination due to brief favorable conditions (e.g., temperature, light, moisture condition of the soil) created by secondary forests established on abandoned sites. This, in turn, depends on the seed biology of seed bank species, such as recalcitrance, dormancy and longevity of seeds (Garwood 1989; Teketay and Granström 1995, 1997). Irrespective of the age of secondary forests, seeds of most species have low viability, which could be related to a number of factors. Infection by micro-organisms possibly reduced viability, consumption of flowers and developing ovules at an early stage of reproductive growth influences the build-up of the soil seed bank (Thompson 2000), and lack of dormancy disfavors the development of persistent soil seed bank (Teketay and Granström 1995; Wassie and Teketay 2006).

Results from the present study agree with previous studies made on soil seed banks in tropical ecosystems. For example, Scholz et al. (2004) studied soil seed banks in tropical dry forests of Palo Verde National Park in Costa Rica in a chronosequence and reported an increasing tendency of species composition with advancement of secondary succession. Miller (1999) examined the effect of deforestation on the soil seed bank of Mexican deciduous forest and found a decline in density of tree/shrub seeds, as observed in the recently abandoned sites in our study. Teketay (1997) assessed the soil seed bank in the forest, gap and arable lands in Ethiopia and found high number of species in the forest while high seed density in the arable land, comparable with the results from site-4 and site-14. Similar to previous studies, which reported few trees species in the seed bank (Bojorquez 1993; Teketay and Granström 1995; Teketay 1997; Miller 1999; Tekle and Bekele 2000; Scholz et al. 2004), we found three tree species in the soil seed banks of site-9 and site-14. However, the similarity between the species composition of the seed bank and that of the standing vegetation was poor (Table 3), as in the case of many other studies (Teketay and Granström 1995; Tekle and Bekele 2000; De Villiers et al. 2003; Scholz et al. 2004; Mengistu et al. 2005; Uasuf et al. 2009). This implies that the seed bank is not likely to be the driving force for successional changes in the vegetation, but secondary forests derived on abandoned sites rely on seed dispersal, as also observed by Guevara et al. (2004) and Beatrijs and Martin (2004). As a whole, the result indicates an increasing tendency of species composition in the soil seed bank as succession advances. The viable seed density of most seed bank species is very low, thus direct seeding or enrichment planting of the desired species is highly recommended to expedite the recovery of secondary forests on these abandoned sites. In addition, installing artificial bird perches may be needed to facilitate inputs of forest seeds through bird dispersal and to accelerate plant succession.

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